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Original Research Article

Does the law of diminishing returns in leaf scaling apply to vines? — Evidence from 12 species of climbing plants

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ABSTRACT

Shapes, sizes and biomass investment per unit area (LMA) of vine leaves are characterized by high diversity that results in variation in leaf arrangement, light harvesting efficiency and photosynthetic activity. There exists a scaling relationship between leaf dry mass and surface area for many broad-leaved plants, and most estimates of the scaling exponent are greater than unity, implying that they follow the "law of diminishing returns", i.e. that larger leaves require progressively greater investments of dry mass and accordingly have a greater LMA. Previous studies have primarily focused on trees and crops and there are few data available for vines. Yet, as vines have lower support investments in stems than self-supporting plants, they can have larger biomass investments in support within the leaves and stronger rise of biomass costs with increasing leaf area. In this study, we chose twelve species of vines (five woody vines and seven herbaceous vines) to investigate the following scientific questions: (i) whether there are significant differences in LMA between woody and herbaceous vines, (ii) whether leaf dry mass and surface area scaling relationships show evidence of diminishing returns in vines. We observed that LMA values of woody vines were significantly higher than those of the herbaceous vines. Leaf dry mass vs. surface area scaling relationship followed the law of diminishing returns in all 12 studied vine species. The existence of diminishing returns indicates that there is a trade-off between leaf surface area expansion and the energy investment for vines to support leaf physical structures.

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1. Introduction

Leaves are the vital plant organs performing photosynthesis and transpiration (Lambers et al., 2008). Through natural selection, diverse leaf shapes have emerged in different plants to maximize the utilization of light and enhance plant adaptation to ambient environments (Li et al., 2017a; Nicotra et al., 2011; Smith et al., 1997). Despite the differences in leaf shape among plants, the scaling relationships of leaf surface area with other leaf measures such as leaf biomass (both leaf fresh mass and dry mass), leaf length, leaf width, leaf perimeter, and leaf thickness have been demonstrated to be similar, following a power law in the form $y = \beta x^{\alpha}$ where β is a scaling constant and α the scaling exponent (Huang et al., 2019a,b; Li et al., 2008; Lin et al., 2018; Niklas et al., 2007; Yu et al., 2019a). Previous studies have shown that the estimated scaling exponents of lamina dry mass vs. lamina surface area for many broad-leaved plants usually fall into a range from 1 to 4/3 (Huang et al., 2019a,b; Milla and Reich, 2007; Niklas et al., 2007). In fact, when leaf fresh mass is proportional to leaf dry mass, the scaling exponents of the leaf fresh mass vs. leaf area and leaf dry mass vs. leaf area are equal (Huang et al., 2019b). Lin et al. (2018) found that the scaling exponent of leaf fresh mass vs. area for the pooled data of 11 bamboo species is approximately equal to 9/8, which is exactly the reported mean scaling exponent calculated for a large number of plant groups in Milla and Reich (2007). Given that $dy/dx = \beta\alpha \cdot x^{\alpha-1}$, the sign of $\alpha-1$ determines whether dy/dx is an increasing function of x ($\alpha-1 > 0$) or a decreasing function of x ($\alpha-1 < 0$) or whether x and y are proportional ($\alpha = 1$). Niklas et al. (2007) collected 1943 species to test the existence of "diminishing returns" in leaf scaling, depicting the phenomenon that the increase in leaf area does not keep pace with that of leaf dry mass, implying that for $\alpha > 1$ the increase in leaf area will require more dry mass investment. In other words, the increase in dry mass per unit will result in a smaller leaf area increment (i.e., diminishing returns). During leaf expansion, the scaling exponent of leaf dry mass vs. area has been found to vary (Liu et al., 2019). Young leaves of *Liquidambar formosana* Hance have a smaller α value, promoting expansion; however, adult leaves have a greater α value, implying a higher cost for ongoing leaf expansion (Liu et al., 2019). Besides leaf scaling, another notable leaf functional trait is the leaf dry mass per unit area (LMA), the quotient of leaf dry mass (M) and area (A; Poorter et al., 2009). Across plant functional types, leaf photosynthetic capacity decreases with increasing LMA, reflecting the leaf economic spectrum, where in one end, fast-growing intolerant species have low-cost short-living leaves with low LMA and high photosynthetic capacity, and in the other end, stress-tolerant slow-growing species have robust long-living leaves with high LMA and low photosynthetic capacity (Wright et al., 2004). On the other hand, LMA and photosynthetic capacity are often positively related along gap-understory and within-canopy light gradients, especially in woody species (Jurik, 1986; Keenan and Niinemets, 2017; Niinemets et al., 2015; Oren et al., 1986). Consequently, LMA has been widely used to characterize the photosynthetic potentials and competitive abilities of plants (Niinemets, 2001; Puglielli et al., 2015; Wright et al., 2004). LMA is also closely associated with leaf scaling as $\mathrm{LMA} = M/A = \beta \cdot A^{\alpha-1}$, indicating that LMA is increasing with leaf area if $\alpha > 1$. However, developmental and environmental controls on LMA have been found to be little affected by leaf allometry (Milla et al., 2008).

Previous studies on leaf scaling have mainly focused on trees, shrubs, crops and some species of bamboo (Huang et al., 2019a,b; Li et al., 2008; Lin et al., 2018; Milla and Reich, 2007; Niklas et al., 2007; Shi et al., 2015; Sun et al., 2017; Yu et al., 2019a,b), but there are few data of leaf scaling in vines. For example, in the study of diminishing returns of Niklas et al. (2007), only 140 leaves were available for vines (4% of total dataset), limiting conclusions about leaf scaling in vines.

Climbing plants, woody vines (lianas) and herbaceous vines, are support parasites that reduce plant growth and survivorship. Woody vines have typically longer and longer-living stems exerting a major influence on their host trees and shrubs (Dillenburg et al., 1993; Fernando and Ernesto, 2009; Schnitzer and Bongers, 2002). Herbaceous climbing plants are significant components in tall grasslands as well as weeds in agricultural fields where they compete with crops for light, water and soil nutrients and can result in the reduction of crop productivity (Rezaul Karim, 2002). In addition, the expansion of some herbaceous vines like *Humulus scandens* (Lour.) Merr (Li et al., 2017b). or woody vines like *Pueraria montana* var. *lobata* (Sasek and Strain, 1990; Carter and Teramura, 1988) can destroy natural ecosystems by strongly reducing community diversity. On the other hand, vines also provide valuable ecosystem services to the society (e.g., raw material for making furniture, fruits and vegetables, pharmaceutical products, and landscape plants in urban green areas). Considering the important roles of vines in the agro-ecosystem, forest ecosystem and urban landscape greening, it is important to gain an insight into leaf functioning in vines. Leaf scaling importantly depends on biomass distribution between major veins and the rest of the leaf lamina (Niinemets et al., 2006; Niinemets et al., 2007a,b). Given that vines have lower investment of biomass in the stem, they might have a greater plasticity for adjusting biomass investment for construction of petiole and within-leaf support than self-supporting plants. If LMA is already large, it might change less (due to carbon limitations or biophysical limitations as leaves with large LMA are expected to have high diffusion resistances for CO_2 and also pentrate little light to leaf interior) when leaf size decreases, i.e. the scaling exponent decreases with LMA increasing.

In the present study, we selected 12 temperate East-Asian vine species, five woody species and seven herbaceous species, to examine: (i) whether woody and herbaceous climbing plants have different LMA values (ii) whether in each species the scaling of lamina dry mass with lamina surface area follows a power-law relationship rather than a proportional linear relationship, (iii) whether the estimated scaling exponents are greater than unity (on the condition that a power-law relationship holds), i.e. whether the data support the existence of diminishing returns for the increase in leaf area with given investment in leaf dry mass, and (iv) whether the diminishing returns are stronger than those so far reported for self-supporting plants.

2. Materials and methods

2.1. Plant material

Fully mature leaves of woody and herbaceous climbing species were collected in 2018 and 2019 from two sites in Nanjing, Jiangsu Province, China (Nanjing Forestry University campus, and White Horse Experimental Station of Nanjing Forestry University). Woody climbing plants included *Trachelospermum jasminoides* (Lindl.) Lem., *Vinca major* L., *Hedera nepalensis* K. Koch var. *sinensis* (Tobl.) Rehd., *Lonicera japonica* Thunb., and *Cocculus orbiculatus* (L.) DC. Herbaceous climbing plants included *Ipomoea triloba* L., *Pharbitis nil* (L.) Choisy, *Dioscorea opposita* Thunb., *Humulus scandens* (Lour.) Merr., *Fallopia multiflora* (Thunb.) Harald., *Polygonum perfoliatum* L., and *Paederia scandens* (Lour.) Merr. (Fig. 1 for representative leaf images of the twelve species of vines). For each species, $\geq$ 290 leaves were randomly collected from different parts of the healthy plants (Table 1 for detailed collection information).

2.2. Data acquisition

Fresh leaves were collected and enclosed in plastic self-sealing bags (28 cm $\times$ 20 cm). The bags were put in a foam box (29 cm $\times$ 16 cm $\times$ 18 cm) with ice to prevent blades from deforming and losing water. We scanned the fresh leaves at a 600 dpi resolution using an Aficio MP 7502 scanner (Ricoh, Tokyo, Japan). After scanning, the leaves were enclosed in Kraft paper envelopes (33 cm $\times$ 24 cm) and dried in a XMTD-8222 ventilated oven (Jinghong Experimental Equipment Co., Ltd., Shanghai,

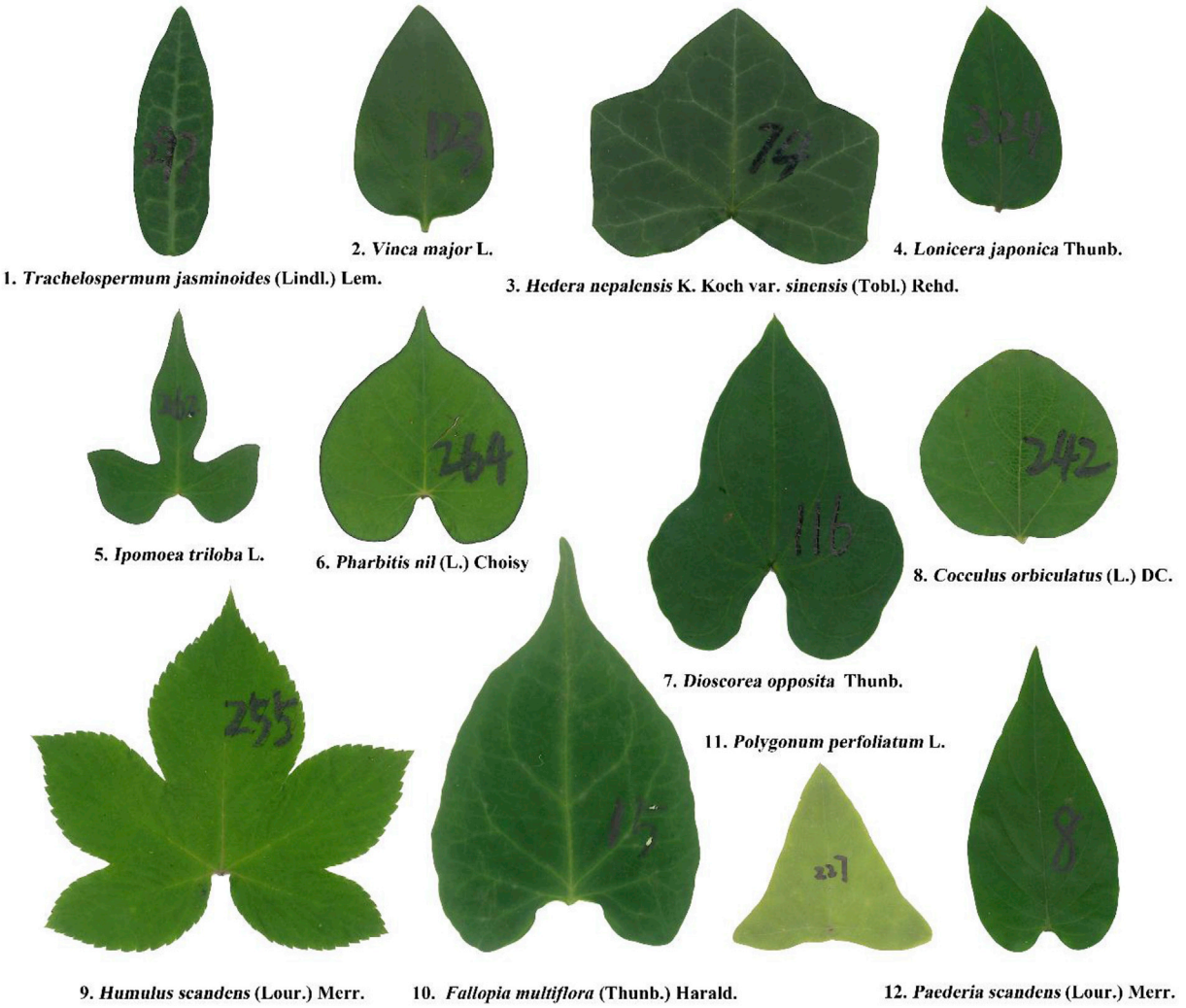

Fig. 1. Representative leaf images of twelve species of climbing plants. The numbers 1 to 12 before the scientific names were used to distinguish different species in the following figures (Table 1).

Table 1
Plant life form, sample size and information of sampling of leaves for twelve species of vines.

Species code[a]	Family	Latin name	Type	Sample size	Collection location	Sampling time
1	Apocynaceae	*Trachelospermum jasminoides* (Lindl.) Lem.	Woody	312	32°04′40″N, 118°48′30″E	20 July 2019
2	Apocynaceae	*Vinca major* L.	Woody	379	32°04′46″N, 118°48′32″E	15 October 2018
3	Araliaceae	*Hedera nepalensis* K. Koch var. *sinensis* (Tobl.) Rehd.	Woody	391	32°04′38″N, 118°48′32″E	23 October 2018
4	Caprifoliaceae	*Lonicera japonica* Thunb.	Woody	344	32°04′50″N, 118°48′34″E	20 July 2019
5	Convolvulaceae	*Ipomoea triloba* L.	Herbaceous	359	31°36′08″N, 119°10′36″E	12 October 2018
6	Convolvulaceae	*Pharbitis nil* (L.) Choisy	Herbaceous	380	31°36′07″N, 119°10′36″E	12 October 2018
7	Dioscoreaceae	*Dioscorea opposita* Thunb.	Herbaceous	338	32°04′48″N, 118°48′44″E	21 July 2019
8	Menispermaceae	*Cocculus orbiculatus* (L.) DC.	Woody	403	31°36′07″N, 119°10′43″E	12 October 2018
9	Moraceae	*Humulus scandens* (Lour.) Merr.	Herbaceous	397	31°36′07″N, 119°10′35″E	12 October 2018
10	Polygonaceae	*Fallopia multiflora* (Thunb.) Harald.	Herbaceous	299	32°05′03″N, 118°48′45″E	9 April 2019
11	Polygonaceae	*Polygonum perfoliatum* L.	Herbaceous	336	31°36′19″N, 119°10′35″E	30 September 2018
12	Rubiaceae	*Paederia scandens* (Lour.) Merr.	Herbaceous	350	32°04′44″N, 118°48′44″E	21 July 2019

[a] Species codes here are the same as those in Fig. 1.

China) at 105 °C for 2 h, followed by drying at 80 °C to a constant mass. Finally, the leaf dry mass was estimated with a ML 204 precision balance (Mettler Toledo Company, Greifensee, Switzerland; measurement accuracy 0.0001g). Leaf area was estimated from scanned images using Matlab (version 2009a) and an R (version 3.6.0; R Core Team, 2019) script for calculating leaf area developed by Shi et al. (2018) and Su et al. (2019), and leaf dry mass per unit area (LMA) was calculated.

2.3. Statistical methods

We tested the significance of the differences in leaf area, dry mass, and LMA among 12 climbing plants using analysis of variance and Tukey's HSD test with 0.05 significance level (Hsu, 1996). To analyze the scaling relationships, data were log-transformed before linear regression analyses to satisfy the criteria of normality of data and residuals (Milla and Reich, 2007; Niklas et al., 2007; Huang et al., 2019a):

$$\ln(M) = \ln(\beta) + \alpha \ln(A), \tag{1}$$

which can be reformulated as:

$$y = \gamma + \alpha x. \tag{2}$$

Here, $y = \ln(M)$, $x = \ln(A)$, and $\gamma = \ln(\beta)$. Parameters γ and α were estimated using reduced major axis regressions (Smith, 2009). We compared the significance of the difference between any two estimates of the scaling exponents using the bootstrap percentile method (Efron and Tibshirani, 1993; Sandhu et al., 2011). All statistical analyses in this study were performed using R (version 3.6.0; R Core Team, 2019).

3. Results

Among the twelve species of vines, *H. scandens* had the largest leaf size (both leaf area and dry mass; Fig. 2a and b), but the LMA of this herbaceous plant was intermediate. Average LMA of five woody vines was significantly greater than that for seven herbaceous vines (Fig. 2c). *Hedera nepalensis* var. *sinensis*, an aggressive understory vine colonizing many tree species, had the highest LMA values. LMA values of the species from the same family were similar (*T. jasminoides* vs. *V. major*, *I. triloba* vs. *P. nil*, and *F. multiflora* vs. *P. perfoliatum*; see Fig. 2c for details).

Strong scaling relationships between leaf dry mass and leaf surface area were observed for each species, because the 95% confidence interval of the slope did not include 0 for each slope (Fig. 3). However, the goodness of fit (for the linear fitting) varied among species. The coefficients of determination in the linear regression models for *T. jasminoides*, *H. nepalensis* var. *sinensis*, *P. nil* and *F. multiflora* (i.e., Fig. 3a,c,f,j; $r^2 < 0.8$) were smaller than those for the other species ($r^2 > 0.8$ for the remaining eight species). Except for *V. major* and *P. nil*, diminishing returns (LMA increasing with increasing leaf size) were

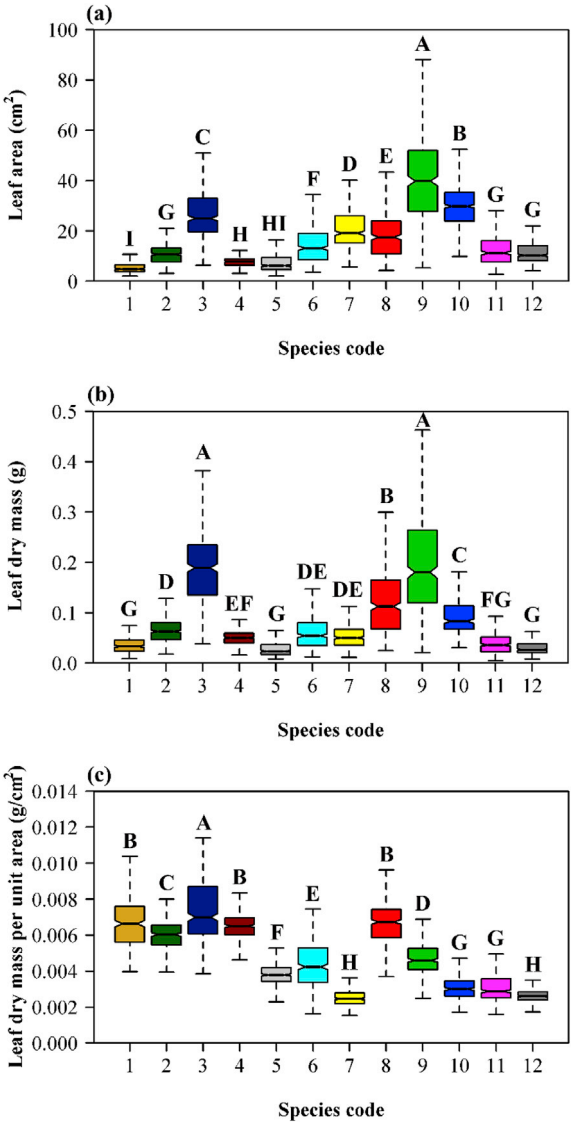

Fig. 2. Boxplots of leaf area (**a**), leaf dry mass (**b**), and leaf dry mass per unit area (**c**). Different letters above the upper whiskers show significant differences among species ($P < 0.05$). Species names corresponding to species codes are provided in Table 1 and Fig. 1.

found to hold for the remaining ten species of vines as the lower bounds of the 95% confidence intervals (CIs) of the estimated scaling exponents for leaf dry mass vs. area, were all greater than unity (Figs. 3 and 4). The 95% CIs of the scaling exponents for *V. major* and *P. nil* included unity, which implies a proportional relationship between leaf dry mass and leaf surface area (constant LMA). The correlation coefficient between the 12 scaling exponents and LMA medians equals −0.47, which means that the scaling exponent decreases with an increased LMA. The average scaling exponent for 5 woody species is 1.07 ± 0.07, and that for 7 herbaceous vines is 1.14 ± 0.08, which also reflects a negative correlation between the scaling exponent of leaf dry mass vs. area and LMA.

4. Discussion

On a basis of a global meta-analysis, Poorter et al. (2009) reported that LMA varies 100-fold among species. They further observed that woody evergreen, perennial or slow-growing species have inherently high LMA (Poorter et al., 2009) consistent with the global leaf economics spectrum (Wright et al., 2004). Our study is in accordance with these observations. *Hedera nepalensis* var. *sinensis* is a woody evergreen perennial vine with gray-green leaves, and has the largest leaf area, leaf dry mass and LMA among four woody climbing plants investigated here (Fig. 2a and b). *Cocculus orbiculatus*, also a woody evergreen perennial vine, has the second largest leaf area, dry mass, and LMA among the four woody vines investigated here. Greater

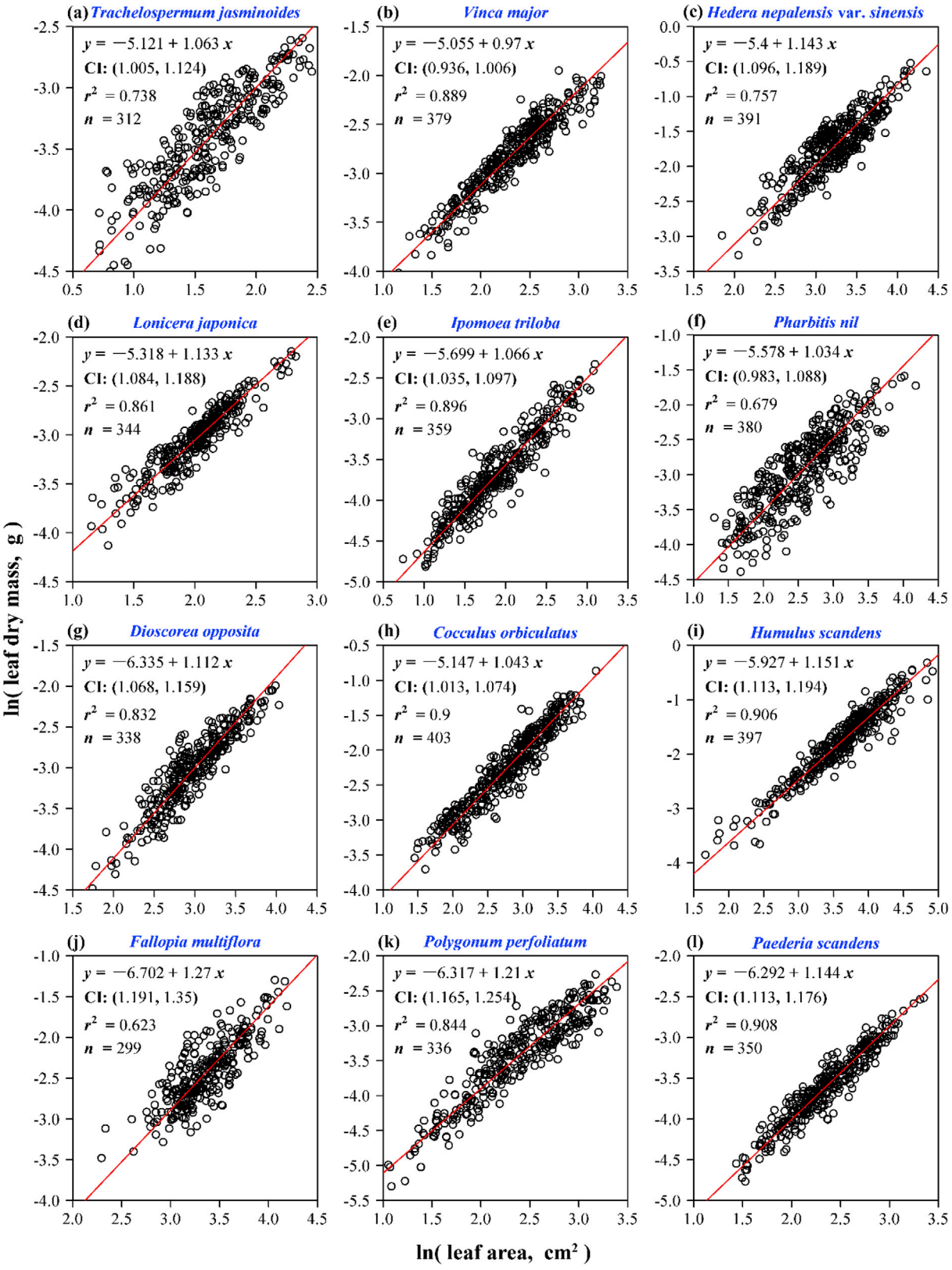

Fig. 3. Scaling relationships between leaf dry mass and leaf surface area for twelve species of vines. Species in panels (**a**–**d** & **h**) are woody vines, and in panels (**e**–**g** & **i**–**l**) herbaceous vines. In each panel, open circles denote the observations of leaf dry mass vs. area, and red straight lines denote the regression lines. *y* represents the natural logarithm of leaf dry mass (g); *x* represents the natural logarithm of leaf area (cm^2); CI represents the 95% confidence interval of the estimated scaling exponent (i.e., the slope) based on 3000 bootstrap replicates; r^2 is the coefficient of determination characterizing the goodness of fit; and *n* is the sample size. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

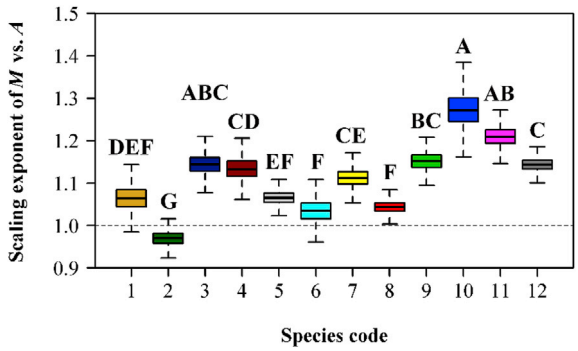

Fig. 4. Comparison of the estimated scaling exponents of leaf dry mass vs. leaf surface area among the twelve species of vines. The uppercase letters A–G on the top of each box denote significant differences among the species ($P < 0.05$). For species names corresponding to species codes see Table 1 and Fig. 1.

LMA is typically associated with higher leaf longevity, but with lower leaf photosynthetic capacity per dry mass (Wright et al., 2004). Higher leaf longevity is an important feature in woody vines allowing them to capitalize on greater biomass investment in support structure. In fact, several woody vines have become invasive in their non-native environments including *Lonicera japonica* from our study that has become a formidable weed in northern America (Evans et al., 2013) or *Pueraria montana* var. *lobata* that is a strong invasive species in northern America and Europe (Hoffberg and Mauricio, 2016; Sasek and Strain, 1990). We believe that the invasive expansion of this vine in northern America might benefit from its strong photosynthetic capacity of its leaves. In addition, *H. scandens* with the largest leaf area and leaf dry mass but the fourth largest LMA (greater than the LMA of any other herbaceous vines studied here) is a weed in many places of China. It can act as a pioneer species in abandoned lands, and can quickly dominate the vacant habitats in flat or mountainous terrains (Chen et al., 2001). In contrast, herbaceous vines with higher leaf turnover can become major weeds in agricultural fields and in early-successional communities, e.g. *Convolvulus* and *Calystegia* spp., but they are typically outcompeted by native species in later stages of succession (Connell and Slatyer, 1977).

Eleven among twelve estimates of the scaling exponent of leaf dry mass vs. leaf surface area fall into a range of 1–1.3 (<4/3), with nine species between 1.0 and 1.2, confirming the values reported for other plant groups (Milla and Reich, 2007; Niklas et al., 2007; Lin et al., 2018; Huang et al., 2019a,b). Niklas et al. (2007) obtained an estimate of 1.196 based on 140 vine leaves. After pooling the data of leaf dry mass vs. area in our twelve vines (totally 4288 leaves), we obtained an estimate of the scaling exponent 1.113 with 95% CI: (1.097, 1.129) and $r^2 = 0.711$ that indicates a reasonably good global fit for the large sample studied here. Li et al. (2008) sampled the leaves from 35 deciduous simple-leaved species, 21 evergreen simple-leaved species, 25 deciduous compound-leaved species at low altitude, and 19 deciduous simple-leaved species at high altitude, which produced a range (1.05, 1.25) for the estimated scaling exponents of leaf dry mass vs. area (a total of 83 temperate woody tree species in Gongga Mountain, southwestern China). Huang et al. (2019a,b) studied the scaling relationships between leaf dry mass and leaf surface area and found that most estimates of the scaling exponents lie between 1.0 and 1.2. They also found that the estimated scaling exponents of leaf dry mass vs. area for five Lauraceae species fall into the same range of 1.0–1.2 while those of five Oleaceae species whose leaf areas are smaller than those of the five Lauraceae species fall into the range of 1.2–1.4. The present study shows that the extent of diminishing returns based on the scaling exponents of leaf dry mass vs. area for the 12 vine plants is not stronger than self-supporting plants such as the species of Lauraceae, Oleaceae, Rosaceae, etc. (Milla and Reich, 2007; Niklas et al., 2007; Huang et al., 2019a,b; Yu et al., 2019a,b). The overall estimates for the scaling exponents fell into to the reported ranges of Milla and Reich (2007) and Niklas et al. (2007).

A scaling exponent of leaf fresh mass vs. leaf surface area has been demonstrated to be stronger than that of leaf dry mass vs. area for each species studied here (Huang et al., 2019a,b). However, as leaf water content is constantly changing during the growth season (even within a day), such variations/fluctuations could lead to different estimates of the scaling exponent using leaf fresh mass. Huang et al. (2019b) found that for six among the twelve bamboo species leaf fresh mass is proportional to leaf dry mass, which has resulted in a non-significant difference between the scaling exponent of leaf fresh mass vs. area and that of leaf dry mass vs. area. However, a significant difference exists between two estimated scaling exponents when leaf fresh mass has an allometric relationship with leaf dry mass. Here, we did not use leaf fresh mass as the response variable because herbaceous vines are easy to lose water that might affect measurement accuracy. However, it does not mean that the above conclusion from Huang et al. (2019b) does not apply to climbing plants. We measured leaf fresh mass of *F. multiflora* investigated here, and found that the estimated scaling exponent of leaf fresh mass vs. area (Fig. 5a) is smaller than that of leaf dry mass vs. area (Fig. 3j). The difference between the two estimated slopes is significant because the 95% CI of the differences between the bootstrap replicates of the former and those of the latter does not include zero (Sandhu et al., 2011). Leaf fresh mass is not proportional to leaf dry mass because the 95% CI of the slope does not include unity (Fig. 5b). This result is consistent with the reported conclusion in Huang et al. (2019b). The ratio of leaf dry mass (M) to fresh mass (FM) has been found to positively correlate with LMA. We found that this conclusion also held for *F. multiflora*, and the correlation coefficient between the M/FM ratio and LMA equals 0.56. It is actually easy to explain this phenomenon. There are scaling relationships

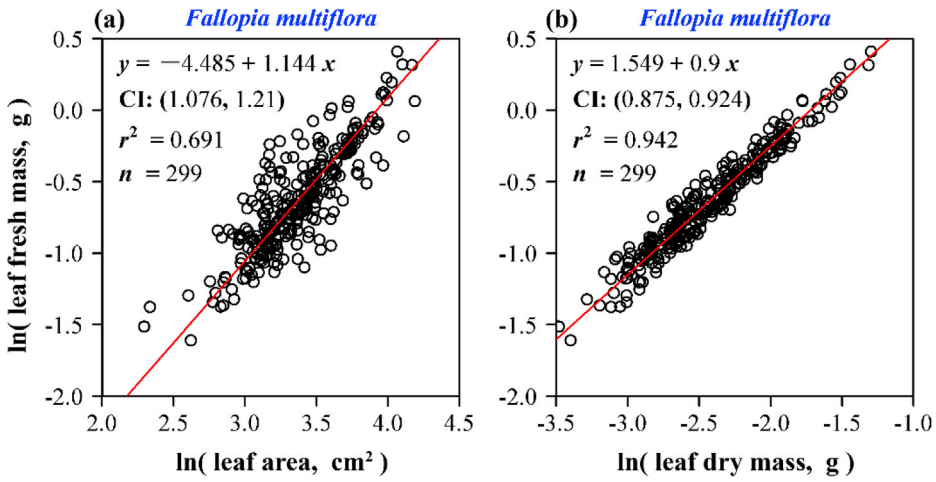

Fig. 5. Scaling relationships between leaf fresh mass and leaf surface area (**a**) and between leaf fresh mass and leaf dry mass (**b**) of *F. multiflora*. In the panels, open circles denote the individual observations and red straight lines denote the linear regression fits. CI represents the 95% confidence interval of the estimated scaling exponents; r^2 is the coefficient of determination (proportion of explained variance); and n is the sample size. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between leaf dry mass and area ($M = \beta_1 A^{\alpha_1}$) and between leaf fresh mass and area ($FM = \beta_2 A^{\alpha_2}$) (Huang et al., 2019a,b). $\mathrm{LMA} = M/A = \beta_1 A^{\alpha_1 - 1}$. Then we can find:

$$M/FM \propto A^{\alpha_1 - \alpha_2} \propto \mathrm{LMA} \cdot A^{1-\alpha_2}. \tag{3}$$

Considering that α_1 and α_2 are both greater than unity (Huang et al., 2019a,b), LMA is an increasing function of A, while $A^{1-\alpha_2}$ is a decreasing function of A. Thus, the ratio of leaf dry mass to fresh mass is actually a trade-off between LMA and $A^{1-\alpha_2}$. Because α_1 is usually greater than α_2 (Huang et al., 2019a,b) overall, the ratio of leaf dry mass to fresh mass increases with leaf surface area increasing. If two scaling exponents are the same, leaf dry weight is then proportional to fresh weight. Because $A^{1-\alpha_2}$ is greater than zero, M/FM is proportional to LMA based on Eq. (3).

In addition, the estimated scaling exponents of leaf dry mass vs. leaf surface area among different vine species (Fig. 4) show a negative correlation with the median of the LMA values ($= -0.47$). However, the correlation coefficient does not approximate 1, which implies a moderate correlation. This could be due to the fact that the scaling exponent of leaf dry mass vs. area is but one measure for the extent of diminishing returns when the increase of leaf area per unit is at the expense of leaf dry mass investment. When the normalized constant (i.e., β) is fixed for different individual leaves of the same species, we observed that larger scaling exponents of leaf dry mass vs. area correspond to higher expense of leaf dry mass investment to increases in leaf area per unit. However, cross-species comparison of scaling exponents makes little sense due to the species specific normalized constant.

Leaf shape is considered to modify leaf venation patterns that could indirectly affect leaf photosynthetic potentials via both biomass investments in support as well as via changes in water availability of single cells (Nicotra et al., 2011; Niinemets et al., 2007b; Runions, 2005, 2017). We showed that the vine stem type, rather than leaf shape, has a significant influence on LMA. Su et al. (2019) demonstrated that leaf shape does not have an influence on the proportional relationship between leaf area and the product of leaf length and width when tested using the simplified Gielis equation (Shi et al., 2015), a special case of a polar coordinate equation that can describe the shapes of many objects (Gielis, 2003), to fit the leaf edges of 20 bamboo species, 12 species of Rosaceae, 5 species of Lauraceae, and 5 species of Oleaceae. After adjusting leaf length by multiplying a coefficient in the equation, the authors found small discrepancies between the actual and predicted leaf area for each species (Shi et al., 2018; Su et al., 2019). Considering that leaf area for many broad-leaved plants is proportional to the product between leaf length and width (Shi et al., 2019a), we think that leaf-shape evolution does not change the proportional relationship between leaf area and the product of two leaf one-dimensional measures but, instead, has substantially changed the proportionality coefficient itself. For instance, *P. perfoliatum* has a triangular leaf shape, with its leaf area proportional to the product between leaf length and width with a coefficient 0.51; the leaves of bamboo that can be described by the simplified Gielis equation (Lin et al., 2016; Shi et al., 2015) also have a proportional relationship with the product between leaf length and width but the coefficients range from 0.68 to $\pi/4$ (Shi et al., 2019b). It is apparent that similar leaf shapes must have similar estimates on the proportionality coefficients of the product between leaf length and width, so leaf shape can play an important role in the leaf-area calculation. However, leaves with similar shapes can have vastly different LMA values. We believe that to understand the implications of leaf shape on foliage functioning, it is necessary to look at leaves with similar LMA and also consider the biomass investment in support and leaf venation pattern.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00830.

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